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BOSTON UNIVERSITY
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Thesis

THE BIOLOGY OF PHRYNOSOMA

by

Warren Hilbourne Southworth

(B.S., Massachusetts State College, 1934)
Submitted in partial fulfillment of the
requirements for the degree of
Master of Arts
1935

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INTRODUCTION

In the summer of 1933 I received a small package which was postmarked in one of the small towns of New Mexico. A friend of mine who was at that time traveling in the Southwest found a "horned toad" and decided to send it instead of a postal card. The receipt of that package marks the beginning of my interest in "horned toads". What kind of toads are they? How could this one be kept alive? What is their natural habitat? The search for the answers to these questions has lead to the writing of this monograph, in which I have attempted to present a compilation of all the available literature concerning the "horned toads".

Although their number is slowly decreasing, the "horned toads" are fairly common in various parts of our southwestern states. For the most part, our knowledge of them is fragmentary. They are a somewhat uncanny group, and many facts concerning their activities are at first thought to be products of the imagination. They do squirt blood from their eyes, and they also change color according to the conditions of their environment. They are lizards even though their outward appearance is somewhat like that of a true toad.

There is need for a well described lizard which can be utilized for instructive and demonstrative purposes. The "horned toads" can easily be kept in captivity and they do not object to being handled gently. They are easy to dissect, and

INTRODUCTION

they can readily be prepared for physiological experimentation. Why not extend our knowledge of them?

THE LIZARDS IN GENERAL AND PHRYNOSOMA IN PARTICULAR

THE LIZARDS' PLACE IN NATURE

Reptiles Past and Present

The history of the reptiles is a very dramatic one, and in order to obtain a clear conception of the lizards' place in nature, we must try to picture the reptiles in all their glory of the Mesozoic period. From an organic standpoint, the Mesozoic was the "Age of Reptiles" for they were at that time the lords of all creation -- the lands, the waters, and, to some extent, the air were dominated by these huge monsters. During this era there lived not fewer than fourteen reptilian orders, many representatives of which attained gigantic proportions, ranging from sixty to eighty feet in length, and weighing thirty tons or more. The dinosaurian world supremacy lasted for nearly one hundred and ten million years, and then the dinosaurs abruptly ceased to be. No one knows exactly why. "The causes of their extinction," says Dr. Newman, "are unknown, and we can only conjecture that they died off for no better reason than that they had run their course, had become stereotyped, senescent, and could evolve no further." On the other hand, perhaps the reason for their extinction is found in the fact that in their time the dinosaurs were the highest expression of animal life, yet the brain in the largest of them did not weigh more than one pound to thirty tons of flesh. This ratio is astounding when one considers that the average

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man possesses three pounds of brain to one hundred and fifty pounds of body weight. Thus, the medieval world was characterized by brute strength and low mentality.

"One of the most inexplicable of events," says Lull, "is the dramatic extinction of this might race, for in the rocks of undoubted Tertiary age not a single trace of them remains." Only the crocodiles, turtles, lizards, and snakes, were sufficiently generalized among reptiles to weather the crisis and live on into the Cenozoic age to be the contemporaries of the birds and mammals which are the dominant animals of that period. At the present the lizards and snakes are the largest reptilian orders, and, although their rôle in nature is relatively unimportant, they are still on the increase in species, though certainly not in size. A moderate estimate of the number of recent species of lizards is about seventeen hundred (Gadow) -- of which ninety-seven are North American species (Ditmars).

For many years biologists have accepted the idea that the snakes and lizards of today were derived from an ancestral prosaurian like Sphenodon, the reputed prototype of all reptiles. Gadow refers to Sphenodon (Hatteria) punctatum as "the last living witness of bygone ages, this primitive, almost generalized type of reptile, this 'living fossil'." Recent studies, however, trace the ancestry of the lizards back to an early lizard-like group of the Permocarboniferous period. This ancestral type, often called Protosauria, was a

very generalized and decidedly lizard-like creature, and was probably ancestral to all subsequent lizards and snakes. Some of the modern lizards, such as Lacerta viridis, have departed very little from that Protosaurian type. Dr. Newman says, "Perhaps this is the secret of their success in outlasting the great reptilian orders that have come and gone; in that the generalized types that do not go to excess of specialization are able to weather the age-long vicissitudes of world change, adapting themselves to new conditions and always plastic enough to adjust themselves to a new environment."

Classification of Modern Reptiles (after Newman and Gadow)

Class --- Reptilia

1. Order --- Prosauria (Rhynchocephalia)

Sphenodon (Hatteria) punctatum

2. Order --- Chelonia (Turtles and Tortoises)

Sub-Order I Athecae

Sub-Order II Thecophora (True Turtles)

Division I Cryptodira

Family 1 Chelydridae (snapping turtles)

Family 2 Dermatemydae

Family 3 Anosternidae (musk turtles)

Family 4 Platysternidae

Family 5 Testudinidae (pond tortoises)

Family 6 Chelonidae (sea turtles)

Division II Pleurodira

Family 1 Trionychidae (soft-shelled tortoises)

3. Order --- Crocodilia

Family 1 Gavialidae

Family 2 Crocodilidae

4. Order --- Sauria (Squamata)

Division I Lacertilia (Lizards)

Sub-Order I Geckones (geckos)

Family 1 Geckonidae

Family 2 Eublespharidae

Family 3 Uroplatidae

Sub-Order II Lacertae (modern lizards)

Family 1 Agamidae

* Family 2 Inguanidae

Family 3 Xenosauridae

Family 4 Anguidae

Family 5 Helodermatidae

Family 6 Aniellidae

Family 7 Zonuridae

Family 8 Xantusiidae

Family 9 Tejidae

Family 10 Amphisbaenidae

Family 11 Scincidae

Family 12 Anelytropidae

Family 13 Dibamidae

Family 14 Gerrhosauridae

Family 15 Lacertidae

Family 16 Varanidae

Family 17 Pygopodidae

Sub-Order III Chamaeleontidae (chameleons)

Division II Ophidia (Snakes)

Family 1 Typhlopidae

Family 2 Glauconiidae

Family 3 Ilysiidae

Family 4 Uropeltidae

Family 5 Boidae

Family 6 Xenopiltidae

Family 7 Colubridae

Family 8 Amblycephalidae

Family 9 Viperidae

* Family Inguanidae includes the genus Phrynosoma

Characters of Reptilia (after Newman and Gadow)

1. The vertebrae are gastrocentrous.
2. The skull articulates with the atlas by one condyle, which is formed mainly by the basioccipital.
3. The mandible consists of many pieces and articulates with the cranium through the quadrate bones.
4. There is an auditory columellar apparatus fitting into the fenestra ovalis.
5. The limbs are of the tetrapodous pentadactyl type.
6. There is an intracranial hypoglossal nerve.
7. The ribs form a true sternum.
8. The ilio-sacral connection is post-acetabular.
9. The skin is covered:
   (a). with scales
   (b). neither with feathers nor with hairs; and there is a great paucity of glands.
10. Reptiles are poikilothermous.
11. The red blood-corpuscles are nucleated, biconvex, and oval.
12. The heart is divided into two atria and an incompletely divided ventricle. It has no conus, but semilunar valves exist at the base of the tripartite aortic trunk.
13. The right and left aortic arches are complete and remain functional.
14. Respiration is effected by lungs; and gills are entirely absent even during embryonic life.

15. Lateral sense organs are absent.
16. The kidneys have no nephrostomes. Each kidney has one separate ureter.
17. There is always a typical cloaca.
18. The eggs are meroblastic.
19. Fertilization is internal, and is effected, with a single exception of Sphenodon, by means of copulatory organs.
20. An amnion and an allantois are formed during development.

Note:

Numbers 1, 2, 3, 7, 8, 14, 16, 18 and 20 separate the reptiles from the Amphibia.

Numbers 9(b), 10, 12 and 13 separate them from birds and mammals.

Numbers 3, 8 and 11 separate them from mammals.

Distinction between Lizards and Snakes

It is almost impossible to find characters which are entirely satisfactory for the distinction between lizards and snakes. The presence of legs in the lizards and their absence in snakes would, at first, seem to offer a criterion for the separation of the two groups. But there are limbless lizards, and there are snakes with at least rudimentary legs. The vast majority of lizards, however, have well developed legs; only a few degenerated burrowing forms being limbless. Unlike the snakes the lizards possess no elastic ligament between the two halves of the lower jaw. Furthermore, the ventral scales of a lizard are usually smaller than the dorsal scales. In doubtful cases a number of characters have to be taken into consideration, and while each of these may fail when taken singly, their combination decides the question. Such critical characters are: (after Gadow)

	Lizards	Snakes
Limbs	2 pairs, 1 pair, or 0	0 or vestigial hind-limbs
Ear-opening	Usually present	Always absent
Eyelids	Mostly movable	No movable eyelids
Tongue	Often not retractile	Always bifid and always retractile into itself
Teeth	Pleuro- or acro- dont (not anchylosed)	Acrodont, anchylosed
Mandibles	Mostly firmly united suturally	Never with suture, mostly with ligamentous connections

	Lizards	Snakes
Columella cranii	Mostly present	Absent
	Mostly with long arches across the temporal region	No bony arches
	Osteoderms common	No osteoderms

Discussion of Sub-Orders of Lacertilia

1. Geckones (geckos)

"The geckos are primitive lizards with the following peculiarities: Four-footed; amphicoelous vertebrae; no bony temporal arches; dilated clavicles; separate parietals; eyes with movable lids; tongue broad, fleshy, protrusible and nicked on the end.

"The geckos are practically cosmopolitan within the warm temperate countries. In the United States they are confined to our Southwestern Pacific regions. They are wonderful climbers. By means of adhesive pads on the toes they are able to ascend the smoothest surfaces such as walls, ceilings, or even window-panes. Adhesion is accomplished by the vacuum-cup principle, but the 'cup' consists of a complicated system of lamellae. They feed on all sorts of small animals, especially insects and spiders. They are absolutely harmless to man in spite of an undeserved reputation for venomousness. Their chief defense consists of an extremely loosely articulated tail, which comes off with great readiness when seized. When cornered and in grave danger, they wag the tail over the body, appearing to offer it for seizure. The enemy is usually satisfied and the tailless gecko proceeds to regenerate another tail, which fortunately it is able to do very readily. Many species have a feeble voice which resembles a repeated click of the tongue, and their name 'gecko' is supposed to be an Indian interpretation of the sound." (Newman)

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2. Chamaelontes (chameleons)

"The chameleons are the most highly specialized of the lizards. The body is laterally compressed; the tail prehensile; the toes are parted in the middle into two groups for grasping, a group of three being opposed by a group of two. Most of them are African or Madagascan, though one species (Chameleon vulgaris) extends into Southern Europe.

"Two characters of chameleons have become notorious: Their ability to change color and their habit of 'shooting' insects with their tongues. Accounts of their color versatility are exaggerated, but the fact remains that they are probably the most effective color changers known, having a range from very light gray to leaf green; and the change can be made in a few seconds. The tongue is capable of 'shooting' a fly at a distance of seven inches and the aim is unerring. Probably the aim is improved by the cruiously modified eyelids which are grown together with the exception of a mere pinhole in the center. Apparently the tongue aims at the exact point of focus of the two eyes. Several signs of racial senescence are displayed by chameleons: their highly compressed bodies, their lack of scales, and the specialized eyes, feet, and tails." (Newman)

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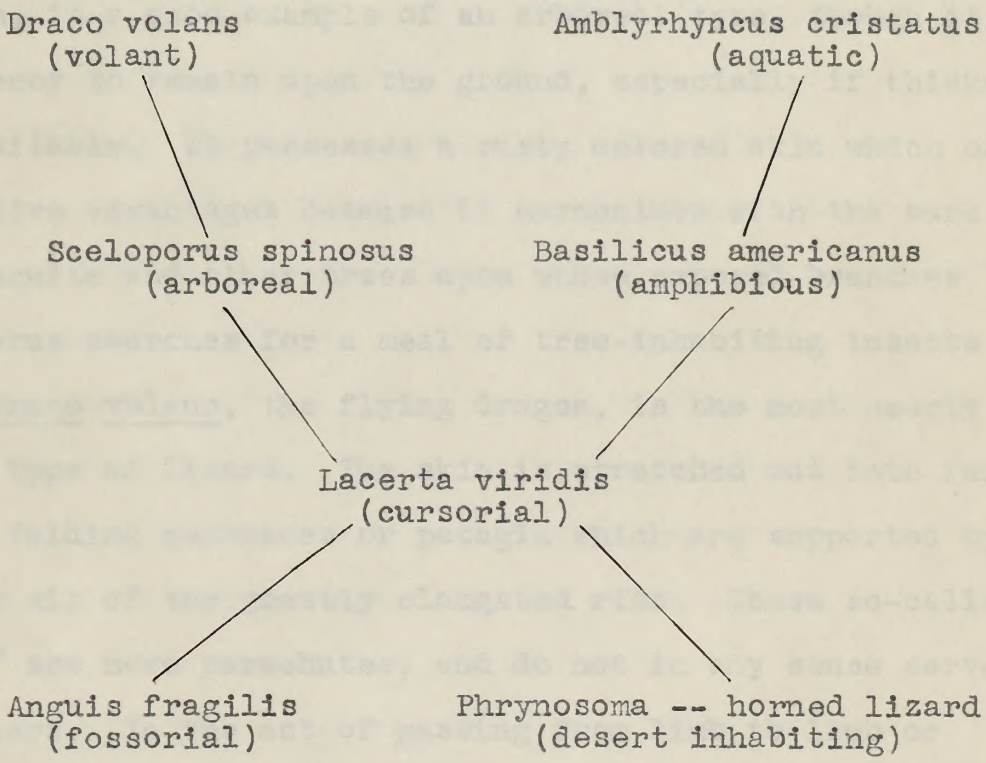
3. Lacertae

"To this group belong the great majority of modern lizards. The members of this suborder are distinguished from the other suborders by the fact that the vertebrae are procoelous and solid, and that the ventral portions of the clavicles are not dilated." (Newman)

In general it may be stated that the Lacertae are a cosmopolitan group, being found in many of the regions between the southern point of Patagonia and the northern lands bordering on the permanently frozen subsoil. It is interesting to note that the tropics contain representatives of both the most highly specialized and developed types of lizards and the most degraded forms. Furthermore, as we approach the tropics, the variety of forms and the number of individuals increase.

Some of the lizards exhibit very unique adaptations to the most diverse environmental conditions. As indicated in Figure 1, from a more or less primitive type, or focus, there radiate types which are specialized for very different habitats and modes of living. Most of the modifications involved in these various adaptations are restricted to the skin, limbs, tail, or tongue, and in many cases the modifications stand in correlation with the kind of food and the way in which it is procured.

Lacerta viridis, the common European "wall lizard", is an excellent example of generalized lizard. In fact, Lacerta exhibits the least specialized condition to be observed among



Adaptive Radiation of Lizards

Figure 1

Adaptive Radiation of Lizards

Figure 1

the living reptiles. It is a small type with long slender proportions, and is a beautiful green above and yellow below. Its moderately long pentadactyl limbs permit the animal to run swiftly upon and over rocks. From such a central type as this have radiated all of the more specialized types.

Sceloporus spinosus, one of the commonest American lizards, is a good example of an arboreal type, though it has a tendency to remain upon the ground, especially if thickets are available. It possesses a rusty colored skin which offers protective advantages because it harmonizes with the bark of the mesquite and other trees upon whose exposed branches Sceloporus searches for a meal of tree-inhabiting insects.

Draco volans, the flying dragon, is the most nearly volant type of lizard. The skin is stretched out into fan-shaped folding membranes or patagia which are supported by five or six of the greatly elongated ribs. These so-called "wings" are mere parachutes, and do not in any sense serve as propellers. In the act of passing from limb to limb or between two adjacent trees, the animal spreads its patagia, leaps into the air, and glides swiftly to a landing place. On the neck are three hooks which, no doubt, enable the aviator to secure a hold when alighting from flight. When the animal is at rest the parachute membranes are folded against the sides.

Anguis fragilis, the "slow-worm" or "blind-worm", is also called in some sections of the country the "glass-worm". These lizards are the true fossorial or burrowing types, and

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Anguis fragilis, the "slow-worm" or "blind-worm", is also called in some sections of the country the "glass-worm". These lizards are the true fossorial or burrowing types, and

they represent the climax of degeneration among lizards. There are numerous gradations between these forms and the more generalized Lacerta, with well developed limbs. The limbless lizards bear a very close resemblance to the snakes, not only in the absence of limbs, but also in the general form of the body and the mode of locomotion. The tail is quite brittle and can be readily removed from the body. If this is done, both the animal and the tail wiggle about vigorously, but only the body is able to resume the journey.

Basiliscus americanus, the American basilisk, is an amphibious type of lizard. It is a large conspicuous lizard, generally about a yard in length. The males are characterized by a very pronounced dorsal crest which extends like a fin over the entire back and two-thirds of the way down the tail. They haunt the branches of trees overhanging the water, and, at the slightest provocation, drop into the water and swim to the shore, using the fin only as a rudder.

Amblyrhynchus cristatus, the sea lizard is as near an approach to the aquatic type as the Lacertilia afford. These rather large, heavy-bodied lizards possess a dorsal fin which extends from the rear of the head to the tip of the tail. Amblyrhynchus is an agile swimmer who often prefers the really dangerous breakers to the enemies on land. The sea lizards have maintained a vegetarian appetite in spite of their seafaring life, and their food mainly consists of seaweeds and other marine flora.

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There dwells in the southwestern part of the United States a lizard which is commonly called the "horned toad". These little creatures, varying from three to seven inches in length, are well adapted to a sub-arid habitat, and for lack of a specific term, we may say they represent a desert inhabiting type of lizard.

The only venomous lizard is the gila monster, Heloderma horidum, a large, heavy-bodied, vividly marked lizard with a skin which possesses closely set, bead-like tubercles. It is provided with grooved fangs which resemble the poison conductor teeth of some of the poisonous serpents. These reptiles do not always eject their venom when biting. The fangs are on the lower jaw bones, and, as they are simply grooved, do not constitute a perfect instrument for the forcible injection of poison.

Molock horridus, the lizard anteater, is a very repulsive looking creature. Its integument bears heavy spines, and its general appearance is quite similar to that of the most bizarre dinosaurs. Only its small size redeems it from utter frightfulness of aspect. The skin of this animal is reputed to be hygroscopic, capable of absorbing moisture from the air.

The so-called monitor, Varanus salvator, reaches a length of seven feet or more. Apart from its great size, the monitor is a very generalized lizard, differing little from the primitive lizard-like reptile, Varanops, which lived in Permian times.

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THE GENUS PHRYNOSOMA

The Name

The members of the genus Phrynosoma are commonly referred to as "horned toads", a name which, in addition to being very inappropriate, is a misnomer. The etymology of Phrynosoma is found in the Greek words "phryne" (a toad) and "soma" (body). The animals included in the genus Phrynosoma possess a body which superficially resembles that of a toad, but their diagnostic characters place them with the lizards. Therefore, from a scientific standpoint the name "horned lizard" is far more appropriate than "horned toad". Furthermore, among the Batrachians there are a number of horned toads -- true horned toads -- which are distinctly separate from the genus of lizards, Phrynosoma.

Characters and Description

The horned lizards are found only in the western portions of the United States and in Mexico, and they are distinct from all other genera of North American lizards. Their much flattened, toad-like bodies; the short tail; the development among most species of sharp, conical horns upon the back of the head and the temples; and the fringes of spiny scales around the edge of the body constitute a very unique set of characters.

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which are irregular in size and shape. Ventrally the scales are small and regular, giving an imbricated appearance. Larger keeled scales cover the front of the arm and thigh. The head is short and somewhat triangular in shape with a sharp projecting margin. The projecting superciliary regions overhang a groove from the occiput to the snout, in which the eye is situated. Small sub-equal scales cover the top of the head and a row of bony spines, variable in length and number, is to be found on the temporal and occipital regions. The projecting superciliary regions bear posteriorly short, sharp scales. Protected by bony processes, and just in front of the interoccipital region, is the median pineal eye. The lower jaw is bordered by large projecting spinous plates. The neck is short, causing transverse gular folds which often cover the auditory aperture. The pentadactyl limbs are short and about equal in length, and the digits are moderately developed, the fourth being the longest. The tail is short, conical, and covered dorsally with the same sort of scales as the back. Posteriorly the ventral scales are keeled. The tympanum may be naked or covered with scales. This character, however, varies within the species. The nostrils are conspicuous and may be either on the line joining the superciliary region with the end of the snout or above this line. A row of femoral pores, varying in number in the different species from seven to twenty, is found in both sexes on either thigh. Those in the male are more highly developed. The presence of enlarged

postanal scales in the male is a dependable character for determining sex. Anal pores are absent. Juveniles may be distinguished by their small size and poorly developed horns." (Bryant, 1911)

Classification

Owing to the difficulty in finding dependable characters, the bases for generic and specific distinction among the horned lizards have not been generally accepted. Bryant (1911) presents the most complete list of the recognized species and subspecies of the genera Phrynosoma and Anota. One grouping used by Cope (1898) and Van Denburgh (1897) based upon the position of the nostrils, divides the species into well defined groups, but those within each group are so unlike in other characteristics and in distribution that even this division is unsatisfactory. A more recent writer, Ditmars (1907) has based his classification upon:

(1) The formations and proportionate length of the head spines.

(2) The character of the spines upon the back and whether these are surrounded by a rosette of smaller spines at their bases.

(3) The character and number of rows (whether one or two) of fringes of spiny scales along the edge of the body.

(4) Whether the scales of the abdomen are smooth or keeled.

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Bryant (1911) has presented an osteological approach to the classification of the horned lizards, and, although the work was mainly concerned with the five different species of

horned lizards inhabiting California and Nevada, he proposes the establishment of two genera, Phrynosoma and Anota. Bryant discovered that in the case of Phrynosoma maccalli the supratemporal openings are absent, and thus he says, "The closure of the supratemporal openings alone seems to justify generic rather than subgeneric separation from the other horned lizards, for this character is without parallel among the Lacertilia." Pratt (1923) in his "Manual of the Vertebrates of the United States" has placed all of the horned lizards in one group, Phrynosoma. It seems quite evident that more specific data are necessary before the various species of horned lizards can be assigned to their proper taxonomic group.

A List of the Recognized Species of the Genus Phrynosoma

(after Bryant)

1.	Phrynosoma asio	Cope	Southwestern Mexico
2.	Phrynosoma blanvillei blanvillei	Bryant (Gray)	Southern California
3.	Phrynosoma blanvillei frontale	Bryant (Van Denburgh)	Central California
4.	Phrynosoma boucardi	Bocourt	Plateau of Mexico
5.	Phrynosoma braconnieri	Bocourt	Southern Mexico
6.	Phrynosoma cerroense	Stejneger	Cerros Island, Lower California
7.	Phrynosoma cornutum	Harlan	Kansas, Oklahoma, Texas, New Mexico, and Northern Mexico
8.	Phrynosoma coronatum	Blainville	Lower California
9.	Phrynosoma ditmarsi	Stejneger	Sonora, Mexico
10.	Phrynosoma douglassi douglassi	Stejneger (Bell)	Northern part of Pacific Region
11.	Phrynosoma douglassi hernadesi	Cope (Girard)	Great Plains and Rocky Mountains
12.	Phrynosoma douglassi ornatissimum	Cope (Girard)	Painted Desert of Arizona
13.	Phrynosoma goodei	Stejneger	Sonora, Mexico
14.	Phrynosoma modestum	Girard	Texas, New Mexico, Utah, Arizona, and southwestern Mexico
15.	Phrynosoma obiculare	Weigmann	Plateaus of Mexico

16.	Phrynosoma platyrhinos	Girard	Lower Sonora and Deserts of the Great Basin from California to Utah
17.	Phrynosoma solare	Gray	Valleys of the Gila and Colorado rivers
18.	Phrynosoma taurus	Duges	Southern Mexico
19.	Phrynosoma maccalli	Van Denburgh	Deserts of the Gila and Colorado rivers
	(Anota maccalli)	Hallowell	

HABITS AND HABITAT OF PHRYNOSOMA

Habitat

Most of the species of Phrynosoma are found in a dry, sunny climate, and usually where there is a sandy soil and very little vegetation. Of the nineteen recognized species and subspecies, all but eight are found in the United States, these eight being distinctly Mexican species (Bryant). The Texas horned lizard, Phrynosoma cornutum, is the most widely distributed and abundant of all horned lizards. It is found from Missouri to Texas and westward to California.

According to Bryant, each species inhabits a rather well defined region and there is little overlapping of areas of distribution. The desert species, Phrynosoma maccalli, appears to be very rare, and is found only in the Colorado Desert, the Gila Desert, and Sonora Mexico. Phrynosoma cerroense is restricted to the Cerros Island, off the west coast of Lower California.

At a temperature on which some reptiles thrive, these creatures of the sub-arid regions are sluggish. They flourish and are most active in a heat that is practically unendurable to the human being. Specimens are able to withstand long exposure to abnormally dry atmospheric conditions. Weese (1917) reports a 2.5 gram animal which was exposed to a constant current of air with an evaporation of 2.4cc per twenty-minute period for a week before death took place.

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The air humidity, air temperature, air current, and soil temperature (surface) are probably the greatest factors in determining the details of seasonal and daily life and the distribution of the various species. According to Weese, Phrynosoma modestum is not essentially a desert and heat loving species. It appears in the greatest abundance in the early summer months, and during the early autumnal rainy season when the atmospheric temperatures do not exceed 32° C., and when the temperature of the substratum in the sunlight does not exceed 38° C.. During these periods the animals move about actively all day, and at night remain in protected nooks under bushes or in the burrows of other small animals, or, occasionally, bury themselves in the loose soil. When the daily maximum temperature becomes greater than 32° C., the period of activity begins earlier in the morning and is terminated toward noon. During the heated part of the day, the lizards are at rest, partly or entirely covered by the loose soil or sand.

In a carefully controlled series of experiments, A. O. Weese (1917) subjected specimens of Phrynosoma modestum to various conditions of humidity, temperature, and rate of flow of the air. The results obtained indicate that, as nearly as could be determined, the optimum evaporation for these lizards lies between 1.5 cc and 3.0 cc per hour. This closely approximates the condition of the air in the natural habitat of the species. During the months of April and May the evaporating power of the air in the vicinity where these creatures live,

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varies from .15 cc (twenty-four hour average) on a rainy and cloudy day, to 1.0 cc on a bright clear day with a light breeze and a temperature of 30° C..

The evaporating power of the air varies with the temperature. In the case of Phrynosoma modestum, the optimum temperature appears to be in the neighborhood of 30° C. when the humidity and circulation of the air is such as to produce an evaporation of 3 cc per hour.

The effects produced by differences in air temperature and humidity are overshadowed by the response to the temperature of the substratum. Weese found that the optimum substratum temperature ranges between 36° and 40° C.. This optimum is usually from five to ten degrees above the temperature of the air. "When animals in a sand-bottom cage were subjected to a continuous blast of air of increasing temperature from above, so as to heat the surface of the soil without greatly increasing the temperature of the lower layers of the soil, the lizards became very restless as the temperature of the soil approached 40° C.. Most of the animals burrowed, or at least flattened their bodies close to the substratum as the surface temperature reached two or three degrees above this optimum." (Weese)

Phrynosoma modestum is abundant on a "mesa" or clinoplane region just above the Rio Grande. On account of its greater moisture content, the surface of the soil in the Rio Grande valley region is cooler than that in the mesa habitat. Like-

wise the surface temperature in the mountains above is cooler because of the moisture in the soil and also on account of the climatic variations due to higher altitude. Phrynosoma douglassi ornatissimum prevails in both of these places, but on the mesa it is found in much smaller numbers. Substratum temperature, therefore, seems to play an important rôle in the distribution of these two species. Of course, careful analysis of all the various habitats must be made before definite conclusions can be drawn.

Breeding Habits

In a survey of the known facts about the breeding habits of Phrynosoma, it seems advisable to begin with the available information concerning the period of gestation. R. W. Shufeldt (1885) captured an adult female Phrynosoma douglassi which he placed in a cage where food was unavailable. At the end of one month of fasting, the lizard exhibited no particular change. After another month without having taken any nutriment, the lizard presented a slightly emaciated appearance, but the body of the animal retained its rotund contour. Shufeldt's original intention was to test the fasting ability of a horned lizard, but towards the end of the third month of fasting, the experiment assumed an entirely new aspect. Within a period of several hours, the lizard brought forth twenty-four young! Each of these was enveloped in a series of membranes which also enclosed a bright yellow yolk about the size of a small pea. Of the entire brood, all except two died either before or a few moments after birth. The mother had been in solitary confinement for three months and the period of gestation, in this case, must have been in the vicinity of one hundred days. Strecker (1907) believes that under natural conditions the time of carrying the eggs is much shorter than one hundred days.

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noted, Phrynosoma douglassi is viviparous. On the other hand, Phyrnosoma cornutum is oviparous. And now the problem is to discuss the nest building and ovulation for this species.

The usual site selected for the nesting burrow is the base of a slanting bank of earth or sand. The female excavates a tunnel which is wide and high enough to work in comfortably, and it is seldom at an angle greater than 75° to the surface of the ground. The digging is done with the fore-feet, while the hind-feet are used to remove the loose earth and bits of stone from the burrow. After the tunnel has been extended to a length of six or seven inches, the female deposits her eggs in a very orderly arrangement. Strecker writes, "As soon as one layer of eggs has been deposited, the lizard fills in around and over them with just enough earth to keep them from contact with each other, and it is really marvelous how hard and firm the earth is packed into the burrow. In one nest examined by me, the eggs were arranged in four layers of six each."

The period of incubation is about forty days, but this depends largely upon the condition of the weather and the location of the nest. The eggs possess a tough, leathery, non-calcarious shell, and all of those in one set are usually of the same shape. However, when several sets of eggs are compared, they show considerable variation, particularly in diameter. According to Strecker, the average Phrynosoma egg measures five-eighths of an inch in length by seven-sixteenths of an inch in diameter. The natural color of the eggs is yellowish-

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white, although they often become darkened by the soil in which they are located.

When first hatched, the young are smooth and tender, and a few minutes after birth they are able to scurry over the ground with an agility equal to that of the parents (Ditmars). Strecker claims that the young receive no care from the mother, "who probably never returns to the spot where she buries the eggs". Edwards, however, observed that a female, which had laid eggs in captivity, became very restless after the eggs were removed from the cage. For two or three days she constantly attempted to get out of the vivarium at the place where the wire screen had been raised to remove the eggs.

Lockwood (1883) has recorded an example of maternal anxiety in Phrynosoma cornutum. In this case the mother lizard made definite attempts to screen the young one from the view of the observer. The young lizard acted wildly and seemed almost unmanageable while the mother tried to direct its movements toward a little depression in the earth. After having guided the young one into a hiding place, the mother made a short, rapid run at right angles to the path of the observer, and she seemed to be trying to withdraw attention from her little one. It is difficult to say whether or not this is the correct interpretation of the lizard's activities, but the act of hiding the offspring certainly suggests at least a small degree of parental care.

Hibernation

The winter months are spent in hibernation, beneath the surface of the ground. In captivity if the lizards are kept in a dark, cool cellar, they go into hibernation. In such a condition the eyes of the animal are tightly closed and the muscles are very rigid. The external temperature of the body is about that of the air (15° - 18° C.). And the breathing is slow and irregular, with several minutes intervening between inspirations.

Moulting

One of the most striking characteristics of the skin of the reptiles is the great thickness of the different layers. This is especially true of the stratum corneum, or outer stratum of the epidermis. In the lizards, snakes, and birds, the stratum corneum is removed annually, and a new one is developed. The process of moulting extends over the entire body and the stratum corneum remains practically intact until it is removed either as a whole or in fragments.

Bruner (1907) presents a classification of the subdivisions of the Saurian epidermis:

I. Stratum corneum
  1. Pellicula epidermica
    a. Stratum sculptum
    b. Stratum internium
  2. Stratum compactum
  3. Stratum relaxatum

II. Stratum Malpighii

"Of these different strata, the pellicula epidermica is especially concerned with exuviation. As described by Blanchard and Leydig, it includes two divisions; a deeper one composed of a single layer of cells, and an outer homogenous stratum sculptum, which is apparently a secretion of the underlying cells. This superficial stratum is ornamented with a peculiar sculpture which varies considerably in different families."

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In the Inguanidae the surface of the pellicula is divided into more or less hexagonal areas which, according to Blanchard, correspond to the cells of the stratum internium. Bruner found that in Phrynosoma these areas are separated by distinct ridges, which bear conspicuous prickles at the angles of intersection. "The hexagonal areas have an average diameter of about 22μ and the prickles may reach a height of 8μ. In this form the prickles show their strongest development on the ordinary scales, while they are small or wanting on the 'horns' and large dorsal spines, where they would probably hinder exuviation." (Bruner)

The first stage of exuviation begins with the development of a new stratum corneum below the old layer. As a part of this growth, a new pellicula is formed, and owing to the development of the prickles and ridges of the new pellicula, the old stratum is isolated and cut off from its supply of moisture and nourishment. The second or mechanical stage of exuviation is effected by the ordinary movements of the body or by other means, such as the swelling of the head.

The exuviation in the head region is the most difficult part of the entire moulting process, particularly because of the close attachment of the skin to the lips and to the openings of the sense organs. The swell mechanism, which causes high blood pressure throughout the head, seems to facilitate exuviation in that part of the body. According to Bruner, the high pressure which distends the capillaries, veins, and sinuses

of the head, produces extensive movements of the lymph. A rich supply of lymph to the epidermis means a more rapid metabolism and an acceleration of the processes of growth which prepare the way for the mechanical stage of exuviation. Furthermore, the high blood pressure causes an enlargement of all the soft parts of the head, and the old inelastic stratum corneum is gradually separated from the more flexible and elastic new layer.

Hoffman (1879) observed that immediately after the old skin has been removed, the new surface presents a rather brilliant appearance. The darker markings upon the dorsum are minutely sprinkled with black and brick red, while the lighter portions remain a pure olive of various shades. The new skin gradually becomes more ashy or dusky, until the hue is like that which the specimens bore previous to moulting.

Stejneger (1892) has suggested that the blood spurting habit is practised only during the time of shedding the skin. But specimens have been observed to go through the entire moulting process without spurting blood, and other specimens have been induced to eject blood when they were not moulting.

The increased blood pressure in the sinuses during the exuviation process, is a probable explanation of the ejection of blood from the eyes at that time. In another section of this monograph the facts about Bruner's swell mechanism which causes a rise of blood pressure within the blood vessels of the head will be reviewed.

Protection

The horned lizards exhibit several distinctive activities which are to some extent protective. The most important of these activities is the color change, in which the animals "imitate" the color of the ground beneath them. According to Dr. Stejneger (1890), in the cedar and pine belts of San Francisco Mountain, the dark surface is closely matched by the general color of the Phrynosoma, and, in addition, their backs are irregularly adorned with greenish and orange colored markings which are "perfect imitations" of the lichens in the immediate locality. When the little creatures are perfectly motionless, they are not easily detected.

Near the rim of the Grand Canyon the ground is covered with small pebbles of variously colored sandstone, ranging from a clayey white to a brick and dark brown, and in that region the specimens are a faithful reproduction of the surroundings. In the black lava belt, east and northeast of San Francisco Mountain, the horned lizards assume a dark ground color which even simulates the gloss of the black lava. Dr. Stejneger made the following observations upon the fresh colors of several specimens: "Ground-color of upper side, including head, satiny black; light markings on median third of body dull, 'Naples yellow', abruptly changing into the yellow ocher of those on the sides; tips of most lateral spines white; tips of largest cephalic spines marbled with ocher; underside yellowish white, densely marbled with blackish; collar, light ocher

yellow."

The horned lizard is one of the most inoffensive and amiable of reptiles, and it usually submits at once without remonstrance. Some of the largest and boldest individuals have been known to make a slight attempt in self defense by biting weakly (Coues 1875), but in most instances the defense act is that of "playing possum". When faced with danger the animal flattens its body, closes its eyes, and remains perfectly still, as if it were dead. In this collapsed state the animal awaits the first opportunity of escape, and then it attempts to flee from the apparent danger.

Another curious knack of the Phrynosoma is that of being able to bury itself in the sand and thereby hide from its enemies. The method involved in this activity is very different from that of other burrowing animals. The plow-shaped head is the principal tool, and the legs are used for forcing the head forward. A gradual lateral and forward wriggling of the body also helps to drive the head beneath the sand, and within a few minutes the body is completely covered with earth. A little shake of the tail casts the sand over that appendage and the burial is complete. Sometimes the lizard digs its way two or three inches beneath the surface. More frequently, however, the back is covered but the head is visible and just level with the surface of the sand. The nasal openings are furnished with a mechanism which facilitates breathing when the nostrils are below the surface of the ground.



A TRAGEDY OF THE REPTILIAN WORLD

From National Geographic Magazine

The most distinctive thing about horned lizards is the circlet of horns which crown the head. According to Coues (1875), the horns afford a slight means of defense. In such cases the head is lowered, the horns set forward, the back arched up, and the whole attitude becomes somewhat like that of a bull in miniature. As evidence that the horns are not without damaging effect, rattlesnakes have been found with the head of the horned lizard protruding through the body wall, and Cope (1898) has recorded the discovery of rattlesnakes with the horns of Phrynosoma caught in the throat.

There are several accounts which indicate the possibility that the blood spurting of horned lizards is a protective device. Professor S. F. Baird states that he has captured many horned lizards in Texas, a few of which were observed to eject a bloody fluid from the inner canthus of the eye. Once while holding one of the specimens at a distance of at least a foot, he received the discharge in his own eye, and he experienced quite a painful sensation as a result. Denton (1892), in a letter to O.P.Hay, says that he received a great surprise when a specimen which he was gently stroking on the back, appeared to look at him as if it were taking aim, and then suddenly shot a stream of blood directly into his eye. Until the blood was removed from the eye, it caused a pain, and the following morning the eye was somewhat inflamed.

In commenting upon this "blood shooting" O. P. Hay (1892) says, "As to the purpose of the habit, it appears to me quite

likely that it is done in order to defend the animal from the attacks of its enemies, although it would not seem probable that blood would hurt the eyes. Nevertheless, a discharge of blood into the eyes of some pursuing bird or snake might so seriously interfere with its clearness of vision that the lizard might make its escape while the enemy was wiping its eyes."



The Road Runner in Action

From National Geographic Magazine

The Horned Lizards in Captivity

In captivity the horned lizards readily eat any living and moving insect or other animal of sufficiently small size. The lizards seem unable to distinguish an insect unless it moves, and, even when an object is in motion, the eyes cannot differentiate between an insect and several moving sand grains. Specimens have been observed to ingest lead shot which was kept in motion by being rolled down an inclined plane.

Sometimes a Phrynosoma will attack a large wooly caterpillar, a grasshopper, an earthworm, or other seemingly difficult objects, and they are swallowed with comparative ease. A. O. Weese (1917) describes the attempt of a medium sized Phrynosoma douglassi to swallow an earth worm two or three times its own size. The Phrynosoma braced its legs and, after several attempts to pull the worm apart, succeeded in swallowing the worm whole, "shaking it in the process much after the manner of a dog shaking a snake". In other instances when the food cannot be swallowed directly, the lizard rubs it to pieces on the sand. On seeing its prey, a Phrynosoma always raises itself well on its legs, probably in order to avoid being bitten. The head is bent toward the prey, and with a rapid snap of the viscid tongue, the insect is conveyed to the mouth of the reptile. This movement is succeeded by a single gulp, and the insect is swallowed alive.

Although horned lizards survive for a long period without water, they are known to drink greedily at times. Ditmars says,

The Horned Lizards in Captivity

In captivity the horned lizards readily eat any living and moving insect or other animal of sufficiently small size. The lizards seem unable to distinguish an insect unless it moves, and, even when an object is in motion, the eyes cannot differentiate between an insect and several moving sand grains. Specimens have been observed to ingest lead shot which was kept in motion by being rolled down an inclined plane.

Sometimes a Phrynosoma will attack a large wooly caterpillar, a grasshopper, an earthworm, or other seemingly difficult objects, and they are swallowed with comparative ease. A. O. Weese (1917) describes the attempt of a medium sized Phrynosoma douglassi to swallow an earth worm two or three times its own size. The Phrynosoma braced its legs and, after several attempts to pull the worm apart, succeeded in swallowing the worm whole, "shaking it in the process much after the manner of a dog shaking a snake". In other instances when the food cannot be swallowed directly, the lizard rubs it to pieces on the sand. On seeing its prey, a Phrynosoma always raises itself well on its legs, probably in order to avoid being bitten. The head is bent toward the prey, and with a rapid snap of the viscid tongue, the insect is conveyed to the mouth of the reptile. This movement is succeeded by a single gulp, and the insect is swallowed alive.

Although horned lizards survive for a long period without water, they are known to drink greedily at times. Dittmars says

that they should be given water in very shallow dishes, sunk in the sand. Bryant observed that a little milk placed in the cage is enjoyed by old and young alike.

In captivity the horned lizards spend a great deal of time in an inactive state with the belly flattened to the ground, the head lowered, and the eyes closed. A flood of sunshine seems to be necessary to keep them in good health. Weese noted that when the sun is not shining directly upon the cage, the majority of the animals (Phrynosoma modestum) are oriented toward the nearest window, and they climb upon the side of the cage toward the light. On cool days they often tilt the body sidewise and orient themselves so that the surface of the back is, as nearly as possible, perpendicular to the sun's rays.

Hypnosis

A condition simulating the hypnotic state can readily be induced in horned lizards. This state which is characterized by immobility may be produced by placing the lizard in a dorsal position and pressing gently but firmly against the ventral surface. Bryant succeeded in "hypnotizing" a specimen by rubbing the animal on the top of the head and between its eyes. Under such treatment the lizard turns its head down, closes its eyes, and apparently goes into a hypnotic stupor, which in some cases lasts for a period of five or ten minutes.

During this inactive state the animal does not exhibit any response to treatment, such as pinching and prodding, which in the normal state produces excitement. Hoagland suggests that such states of tonic immobility are due to the stimulation arising from a sudden change in the tension of the postural muscles, and that the release of adrenin is of some importance in determining the duration of the condition.

SOME PHYSIOLOGICAL ASPECTS

Blood Cell Formation

From an evolutionary standpoint, the formation of blood cells in the spleen of Phrynosoma is of particular interest. In the Amphibia the spleen is the chief organ for renewing all kinds of blood corpuscles, particularly after hibernation. In most reptiles the important center of blood cell formation has shifted from the spleen to the marrow of the bones, and although the spleen participates in the formation of new corpuscles, the majority of the blood cells arise in the bone marrow. The birds exhibit a complete shift in the chief locus of blood cell formation, from the spleen to the bone marrow. According to the observations of H. E. Jordan and C. C. Speidal (1929), the blood cell formation in Phrynosoma represents an intermediate stage between that of the Amphibia and that of the Reptilia in general. In Phrynosoma the bone marrow is active in the formation of new blood corpuscles, but the spleen is the chief locus for the manufacture of erythrocytes, thrombocytes, monocytes, and granulocytes.

Jordan and Speidal discovered that in the spleen of Phrynosoma, the lymphocytes are derived from a mass of irregularly shaped mesenchymal cells, and that the lymphocytes, in turn, are ancestral to all the other types of blood cells -- erythrocytes, thrombocytes, monocytes, and granulocytes. A graded series of tissues representing granulocytopoiesis within the spleen suggests that the basiphils represent abortive

SOME PHYSIOLOGICAL ASPECTS

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eosinophils in which the granules failed to ripen properly. Other processes of haemocytopoiesis, as shown by sections of spleen tissue, exhibit complete transitional series between lymphocytes and the various blood corpuscles. However different the various forms of corpuscles may be in the adult condition, they arise from the lymphocytes.

The Color Change

In an earlier section of this monograph it was pointed out that the horned lizard represents a fine example of protective coloration. Now the problem is to see just how the lizard changes its color in accordance with the surrounding conditions of temperature, light, and color of the substratum.

First of all, the writer will attempt to describe the various color changes which occur in the skin of horned lizards. The most general color adjustment is that in which the lizard simulates the color of the environment in which it lives. Whether it be in the vari-colored mountain districts, in the lava belt, or on the bleached sand of the desert, the horned lizard will gradually change its color until it harmonizes with that of the ground. When one of these animals is transferred from a light substratum to a darker substratum, the color adjustment in the skin becomes noticeable within forty-eight hours. This adaptive reaction depends upon stimuli received through the eyes. If animals which have been kept on a bed of dark cinders are blindfolded and transferred to a bed of white sand, the lizards so treated will retain the dark color, although they are kept upon the light colored background for several weeks.

Upon this adaptive color change is superimposed the daily rhythm of color change. Let us imagine that we are watching the color changes of several horned lizards while they repose on the whitened desert sand. It is morning, two or three hours

after sunrise, and the color of the lizards is slightly darker than that of the sand. While the sun climbs higher and higher and the heat becomes almost intolerable, the skin of these creatures becomes lighter, and its color very nearly approximates that of the sand. Shortly after midday the color of the skin begins to return to a darker shade, and by late afternoon the color is like that which we saw in early morning. Now the sun has set, and as evening approaches another color change gradually becomes evident, and the animal again is pale. This daily cycle of color changes varies within a margin which at either extreme is only slightly lighter or darker than the background.

If we handle any of the lizards, try to pry open their mouths, or pinch their tails, an immediate color change occurs. Any noxious stimulus -- causing nervous excitement -- will produce a paleness over the entire body. Likewise, a male lizard in the act of copulation will tend to become very pale at a time when the skin color of the other animals in the same pen is very dark. The color reaction produced by noxious stimuli is a dominant one, occurring irrespective of the daily cycle and the color of the environment.

The skin of a horned lizard contains pigment cells, melanophores, beneath which is located a more or less opaque guanine layer. The integumentary color changes are due to the migration of the pigment within the pigment cells or melanophores. The numerous processes extending from the melanophores

form a very close network on the proximal face of the epidermis. When the dark pigment granules migrate distally, the general appearance of the skin becomes darker. On the other hand, when the pigment is retained within the body of each cell, the skin takes on a lightish appearance because the refractile particles of the guanin have thus become exposed to the light. The contraction of the melanophore pigment results in a light-colored skin; an expansion of pigment produces a dark-colored skin.

There appears to be a similarity between the contraction and expansion of melanophore pigment and the tonic changes in smooth muscle. One of the outstanding characteristics of melanophores is their power to produce a condition of prolonged contraction or expansion of the pigment with no apparent evidence of fatigue. The main distinguishing and important characteristic of plain muscle lies in its ability to develop a condition of maintained shortening and increased tension or tonus (Howell 1933). Spaeth (1916) has demonstrated that many of the physiological reagents which produce a contraction of the smooth muscle also produce a contraction of the melanophore pigment. If this view of the melanophores be taken, the contracted state may be called that of increased tonus; the expanded state that of decreased tonus. The state of tonus of the melanophores is dependent upon the existing conditions within and about the cell, and any change in these conditions will upset the equilibrium. In such a case a new point of

equilibrium will be established and the melanophore pigment will receive a different distribution within the cell. "By changing the balance of the factors which affect the melanophore, its tonus is changed." (Redfield 1918)

The remainder of the discussion of the melanophores will be concerned with the factors which influence the melanophore tonus and with the coordinating mechanism of the melanophore reaction. According to the experiments of Redfield (1918), some of the color reactions are due to a direct stimulus of the melanophores. Irrespective of illumination, high temperatures produce ~~an expansion~~ a contraction of the melanophore pigment. At intermediate temperatures (20° - 30°C.) the state of the melanophores is conditioned by the illumination -- light causing an expansion and darkness a contraction of pigment.

Now we have the information with which to explain the daily cycle of color change in the horned lizards. "The expansion of the pigment in the morning is due to the stimulation of light. The heat of midday causes a contraction in spite of the light, but as the air cools in the afternoon, the light effect again dominates and the pigment expands. When the light fails, at night, the pigment becomes contracted as a result." (Redfield 1918)

The effects produced by the environment and those produced by illumination should not be confused. Adjustment to a light background requires contraction of melanophore pigment, whereas light, under conditions of intermediate temperatures,

causes an expansion of pigment. Furthermore, the environmental stimuli are dependent upon a specific receptor, the eyes, whereas light acts directly upon the melanophores.

How do stimuli arising from the environment and noxious stimuli act upon a restricted area of the body, and at the same time cause a reaction of pigment over a large surface of the body? This integration is accomplished by adrenal secretion and the direct action of the nerves. Either mechanism alone is capable of causing the melanophore pigment to contract. (Redfield)

The circulation of blood in the skin plays an important rôle in the activities of the melanophores. In the first place, the blood is active in maintaining the metabolic processes of the melanophores. Interruption of the circulation in a part of the body where the melanophore pigment is expanded causes the pigment to contract, and in the course of two hours the ligatured part becomes paler than the rest of the body. Secondly, the blood contains a hormone, adrenin, which causes a contraction of melanophore pigment. In order to study the effects of adrenin upon the melanophores, the effects due to the nervous system must be eliminated. For reasons which will be evident later, the destruction of the spinal cord between the eighth and thirteenth vertebrae prevents the contraction of the melanophore pigment which normally follows noxious stimuli. In a lizard which has received such treatment, the blood system must be responsible for the distribution of a substance which

will cause any contraction of the melanophores over the entire body.

If the adrenal blood vessels are obstructed, no change in the tonus of the pigment cells is observed, upon stimulation of the adrenal gland, until after the ligature has been removed. Furthermore, after removal of the adrenal glands, no contraction of the melanophore pigment is distinguished, even after the application of various noxious stimuli. The evidence that adrenin is effective in melanophore contraction is demonstrated when extracts from the adrenal glands of a horned lizard are injected into living specimens. If adrenin is produced in the circulation of the horned lizard during nervous excitement and if adrenin is responsible for the contraction of the melanophore pigment at this time, one might expect to find the pigment contracted under other conditions which are known to activate the adrenal glands, and such is the case -- asphyxia, ether, anaesthesia, and poisoning by morphia and nicotine all make for the contraction of melanophore pigment.

In order to study the nervous control of the melanophores one must eliminate the action of the hormones upon the part of the body under examination. Thus, in an animal from which the adrenal glands have been removed the proper conditions have been established. Then if the spinal cord is transected at the thirteenth vertebra, the coordinating effects of the nerves may well be demonstrated. A couple of days after the operation the melanophore pigment is uniformly expanded, but the condition of

the pigment changes when a stimulus is applied to the mouth. The back, anterior to the point of transection, becomes very distinctly paler, while the melanophore pigment of the posterior part of the body remains fully expanded.

After a series of reflex experiments, Redfield concluded that "in the region between the eighth and thirteenth vertebrae are located nervous structures, perhaps 'nerve centers', through which those nerve impulses pass which cause a contraction of the melanophore pigment." Nervous impulses reach this part of the spinal cord from either end. Impulses originating in the color of the environment or the substratum are probably conducted over the optic nerves and thence posteriorly through the brain and spinal cord. Noxious stimuli, no doubt, pass along the sensory fibers.

Nervous impulses pass from this region either to the adrenal glands or to efferent nerves which connect directly with the melanophores. Since the portion of the spinal cord anterior to the eighth vertebra cannot produce a reaction in the melanophores, and the portion posterior to the thirteenth vertebra is unnecessary for reaction, those impulses which pass to the adrenal glands must traverse nerves which leave the cord between the eighth and thirteenth vertebrae. The courses of those impulses which pass directly to the melanophores are determined by tracts which run posteriorly and anteriorly, within the spinal cord, to the segments of the body in which the affected melanophores lie. From these points they leave the

cord to traverse segmental peripheral nerve-trunks to the melanophores. Impulses which pass along the peripheral nerves are carried by fibers of the sympathetic division of the autonomic nervous system.

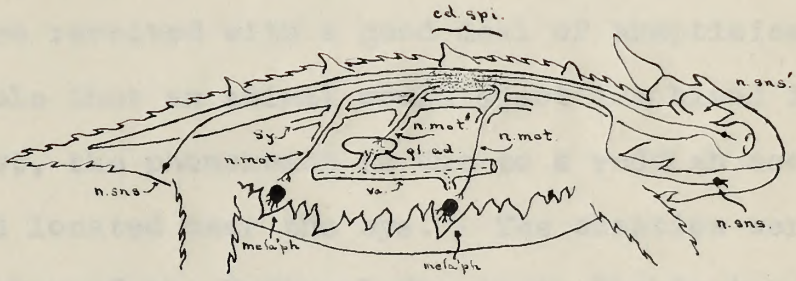
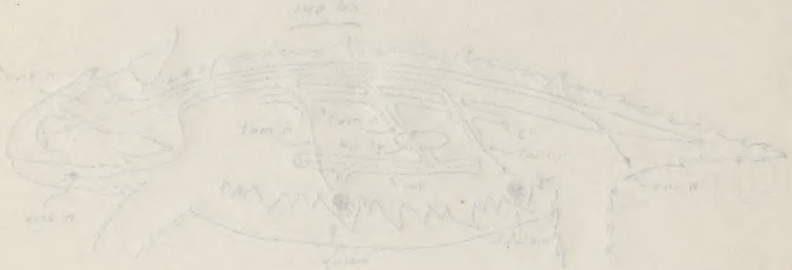


Diagram of the Mechanism Coordinating the Melanophores of the Horned Lizard

Noxious stimuli are carried along the sensory neurons, n. sns., and photic stimuli are carried along other sensory neurons, n. sns'., to a region of the spinal cord between the eighth and thirteenth vertebrae, cd. spi.. From there impulses pass out along motor neurons, n. mot'., to the adrenal gland, gl. ad.. The secretion of adrenin so induced is carried by the blood-vessels, va., to the melanophores, mela'ph.. Other impulses travel along other motor neurons, n. mot., which pass through the sympathetic nervous system, sy., directly to the melanophores. The melanophores are affected in addition by illumination and temperature, the action of which is independent of the coordinating systems of the body.

(after Redfield)

W.H.B



The Blood Spurt

The Mexicans have a small creature which they call the "sacred toad" because it sheds tears of blood. This "sacred toad" is none other than our own "horned toad" or "horned lizard". For many years the stories about this blood spurting activity were received with a good deal of skepticism -- "It isn't probable that an animal would eject its blood in this way. At most, the phenomenon is due to a reddi sh secretion from a gland located near the eye." The skeptics were wrong!

O. P. Hay of the National Museum in Washington D.C., in his report for 1892 presents an account which corroborates, for the most part, the previous descriptions of the horned lizards' blood spurting activities. One day in August while one of the museum specimens was in the process of moulting, Hay observed that the animal was encountering difficulty because the skin was dry and adhered closely. He conceived the idea that a little moisture might facilitate matters, and he submerged the little creature into a basin of water. Hay writes, "The first surprise was probably experienced by the Phrynosoma, but the next surprise was my own, for on one side of the basin there suddenly appeared a number of spots of red fluid, which resembled blood." Yes, a microscopic examination of this fluid proved that it was blood, and there were ninety splotches of it on the sides of the vessel. "The next day while I was holding the lizard between my thumb and middle finger and stroking its horns with my forefinger, a quantity of blood was suddenly

thrown out against my fingers, and this blood came directly from the eye." Upon taste examination the blood revealed a slight musky flavor. Further teasing failed to induce the animal to repeat the act.

There are several authentic reports in regard to the blood spurting process of horned lizards. Each of these reports indicates that fear and vexation are precursory conditions. Prodding, handling, and placing the animal on its back are some of the ways in which the blood spurting can be invoked. Hay (1892), Underwood (1892), and Ditmars (1907) have presented descriptions of this cruious device, and all three of these observers agree in regard to the conditions preceding the ejection of blood, the amount of blood ejected, the successive number of times in which a lizard can be induced to spurt, the repidity with which the activity is executed, and the place from which the jet seems to flow. Each of the reports, however, includes something which is not included in the other two. Hay notes that the museum specimen upon which his observations were made was in the process of moulting. Underwood states that his animal after spurting became limp and collapsed, and remained in a stupor for some time (between five and ten minutes), and, when handled, behaved as if dead. Ditmars says that just preceding the flow of blood from the eyes, the animal -- Phrynosoma obiculare -- threw its head slightly upward, its neck became rigid, and the eyes bulged from the sockets. Then accompanying the blood spurt there was a distinct sound which

is very much like that produced when one presses the tongue against the roof of the mouth and forces a small quantity of air forward.

Although this blood spurting is one of the strangest processes in the animal kingdom, it seems to have been overlooked by the investigators. Hay (1892) states, "The most probable theory regarding the matter seems to be that there is lodged in the head, on each side, a blood sinus, a portion of whose wall lies in the inner surface of the eyelid. The sinus is probably surrounded with muscular tissue of sufficient force to cause the thin wall in the lid to be ruptured and the blood to be ejected to a considerable distance. If this is the actual structure of the apparatus the rupture would soon heal and all things would be ready for the next time. Now, on turning up the upper lid of the eye of the living specimen, the inner lining is seen to be very dark, not with pigment, apparently, but as if there were a quantity of blood there contained in a thin-walled vessel. However, if such an explanation is the correct one, the sinus, in order to contain sufficient blood, must be continued back into the head some distance." Hay raised the question, but it remained for Bruner (1907) to begin the search for an answer.

The swell mechanism described by Bruner offers a partial solution to the problem concerning the ejection of blood from the orbit of Phrynosoma. Just as Hay suggested, there are large sinuses on each side of the head which play an important

rôle in the swelling process, and there are distinct muscles which cause a constriction of these sinuses and adjacent veins, and thereby produce a great rise of blood pressure. The vena jugularis interna probably carries nine-tenths of the blood from the face and cranium, and it connects anteriorly with the sinus orbitalis. In the region where the jugular vein passes from the head to the neck, Bruner found a striated muscle, m. constrictor venae jugularis internae, which surrounds the vena jugularis interna for a distance of about 1600 μ. In Phrynosoma some of the fibers of this muscle are attached to the parotic process which is formed chiefly by the occipitate laterale and the opisthoticum, and is situated directly lateral to the jugular vein. The muscle fibers extending from the parotic process to the jugular vein are arranged in two fan-shaped bundles, one above and the other below the vein. These fibers together with other muscle fibers, which both begin and end in the wall of the vein, form a spiral muscle which in outline looks very much like a barrel. The middle portion of the muscle includes seven or eight layers of spiral fibers, while the number of layers is gradually reduced toward the ends of the muscle. Inside of the spiral fibers the muscle contains one or two layers of longitudinal fibers which are deeply imbedded in the wall of the vein. Opposite the parotic connection of the muscle the vena cerebralis posterior penetrates the muscle in order to connect with the jugular vein, and a few of the muscle fibers are inserted upon the wall of the vena cere-

bralis posterior.

The innervation of the m. constrictor venae jugularis internae is assigned to a set of small nerves which Bruner designates nervi tumefactores capitis. The fibers of the tumefactores can be traced to the ganglion glossopharyngei and thence to the ganglion radicis vagi.

The sinus orbitalis is located anterior to the vena jugularis interna, and its drainage territory is very extensive. Thus, when the jugular vein is closed by the action of the constrictor muscle, blood accumulates in the sinus orbitalis and the venous blood pressure gradually rises. Within the cranium the walls of large sinus-like veins are supported by the rigid cranium, and the enlargement of these veins soon reaches a maximum. In the extra-cranial sinuses, such as the sinus orbitalis, the distension increases as the blood pressure rises, and the total enlargement may be very great.

The results produced by the contraction of the m. constrictor venae jugularis internae are augmented by the action of the muscle which Bruner calls m. protrusor oculi. In Phrynosoma this is a relatively short and stout muscle. "Its dorsal portion arises from a bony process which extends forward from the lateral part of the basisphenoid bone. Its posterior fibers terminate in a fascia which is inserted partly on the trabecula cranii and partly on a posterior process of the subiculum infundibuli of Gaupp. By contraction of the posterior portion of the m. protrusor oculi, the ventral fascia is

elevated and the vena jugularis interna is compressed against the eye muscles, which form a sort of cushion between the vein and the subiculum infundibuli. The anterior part of the muscle elevates and gives tension to the fascia which underlies the sinus orbitalis." As the walls of the sinus orbitalis gradually become distended, the pressure against the bulbus causes the eye to be protruded.

The protrusion of the eye seems to take place in a fairly definite series of stages. At first there is the distension stage during which the sinus orbitalis gradually fills with blood and the bulbus is moderately protruded. Then there is a high pressure stage which begins with a sudden protrusion of the eyes. The eyelids remain closed, and the membrana nictitans becomes more or less protracted as a result of the great blood pressure. According to Bruner, in the first stage of protrusion, the observed effects are due in a large measure to the contraction of the m. constrictor venae jugularis internae. In the second stage the m. constrictor venae jugularis internae maintains its tonus, while the contraction of the m. protrusor oculi entirely closes the outlet of the sinus orbitalis and at the same time pushes against the membranous wall of the sinus and raises the blood pressure to a high level, thus causing the sudden orbital protrusion.

In this swell mechanism described by Bruner we have an apparatus which may be concerned with the ejection of blood from the eyes of Phrynosoma. "The sinus orbitalis forms a

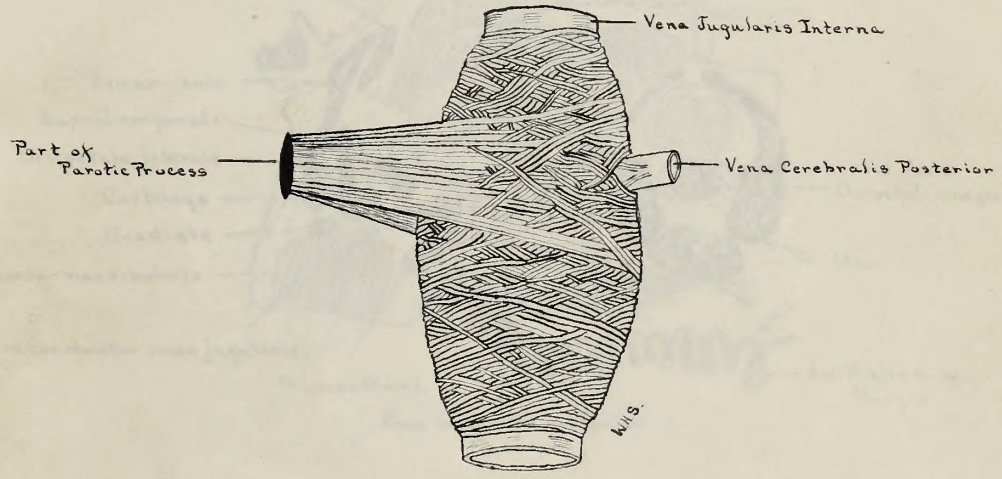
suitable reservoir for the reception of the blood to be ejected. This sinus may be filled with blood by contraction of the m. constrictor venae jugularis internae. The m. protrusor oculi could probably furnish sufficient force to cause the ejection of the blood, but if necessary, this muscle might be assisted by the smooth muscle of the orbit, m. compressor sinus orbitalis."

Bruner discovered that the muscle for constricting the vena jugularis interna is found in association with the enlargement of cephalic veins and sinuses of many reptiles. The wide distribution of the swell mechanism suggests that the mechanism is not primarily for the ejection of blood, and "points to the existence of an undiscovered function of fundamental importance in the life of its possessors."

In their embryonic development the fibers of the m. constrictor venae jugularis internae arise in place, and do not originate by a separation from one of the larger adjacent muscles. "This observation," says Bruner, "indicates that the muscle is not a recent acquisition, but has been derived by modification and change of function, from an earlier muscle which occupied a closely related position. Some of the lower Amphibians are provided with a system of muscles which arise from the parotic region of the head and insert on the dorsal cartilaginous branchial arches."

In the preceding pages of this section, the author has attempted to present a review of the known facts about the

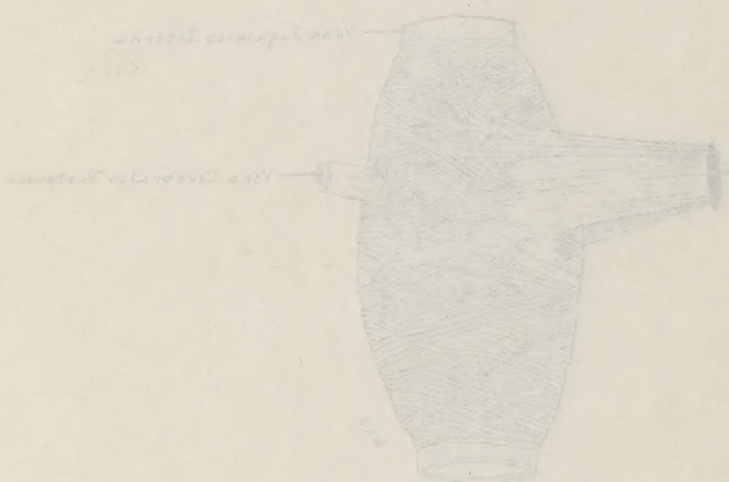
swell mechanism and an indication of the possible ancestry of this apparatus which is found in many of our modern reptiles. Only one of the possessors of a swell mechanism, Phrynosoma, is reputed to eject blood from its orbital region. Whether this apparatus is intended as an aid to the moulting process, or whether it is a protective mechanism which has found its ultimate expression in Phrynosoma, remains to be determined.

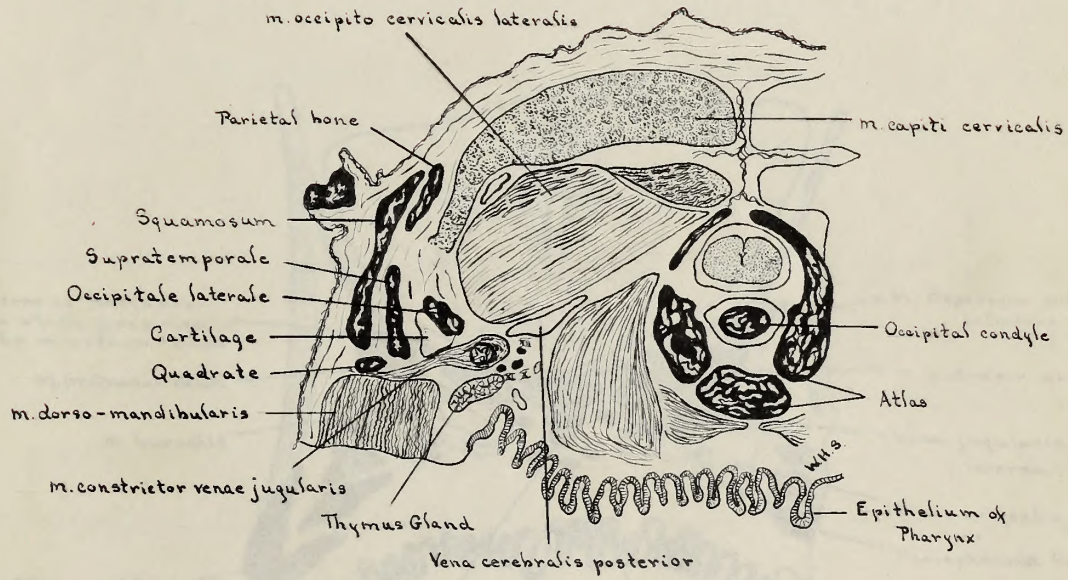


Muscularis Constrictor Venae Jugularis Internae of

Phrynosoma cornutum ----- Left side

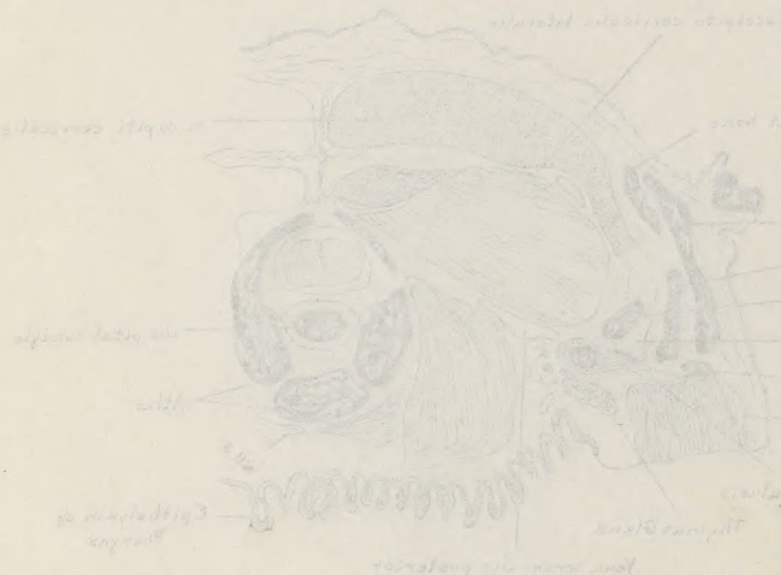
from above X 32 (after Bruner)

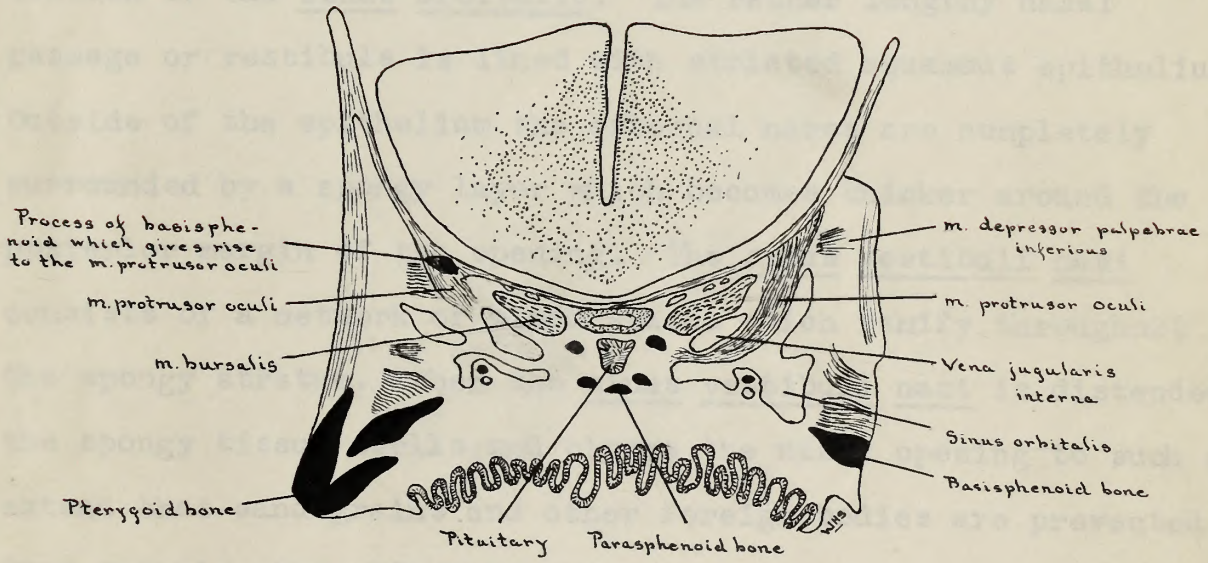




Transverse Section Through Parotic Process, Showing General Relations of M. Constrictor Venae Jugularis Internae

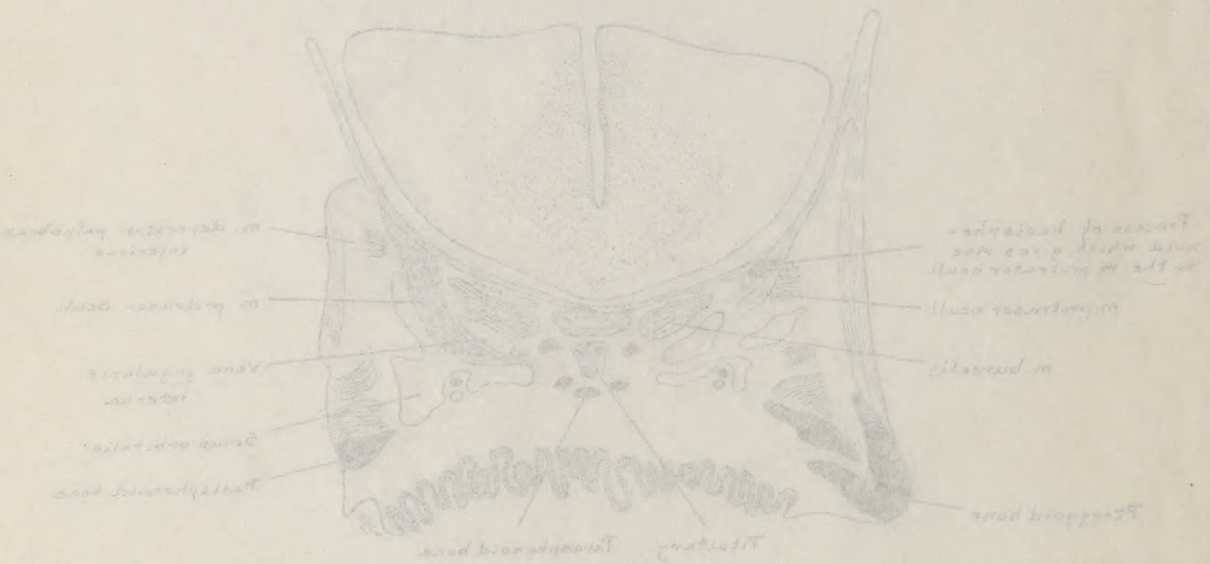
(after Bruner)





Transverse Section of Phrynosoma cornutum through the Region of the Musculus Protrusor Oculi

(after Bruner)



The Nasal Openings

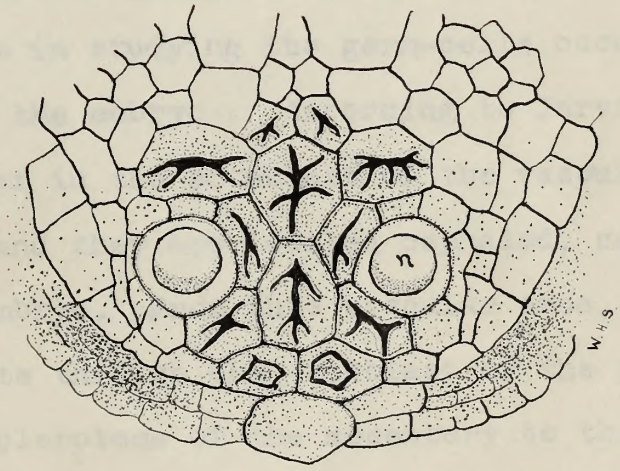
In another section of this paper, the burrowing habit, which is peculiar to the horned lizards, was described, and it was pointed out that the nasal openings of these animals are provided with a mechanism which permits the lizard to breathe easily when the head is below the surface of the ground. This mechanism is quite similar to the one responsible for the distension of the sinus orbitalis. The rather lengthy nasal passage or vestibule is lined with striated squamous epithelium. Outside of the epithelium the external nares are completely surrounded by a spongy layer which becomes thicker around the posterior margin of the opening. The sinus vestibuli nasi consists of a network of blood spaces which ramify throughout the spongy stratum. When the sinus vestibuli nasi is distended the spongy tissue swells and closes the nasal opening to such an extent that sand grains and other foreign bodies are prevented from entering the olfactory chamber.

According to Bruner, "When the eye of the lizard is protruded, a sympathetic swelling may sometimes be observed in the region of the sinus vestibuli nasi". In addition to a sympathetic swelling in this region, there is provision for local control of the sinus, and the external nasal openings may be constricted or closed without interfering with the other functions of the head. The local control of the sinus is probably vested in the smooth muscle fibers of the blood vessels.

The Nasal Openings

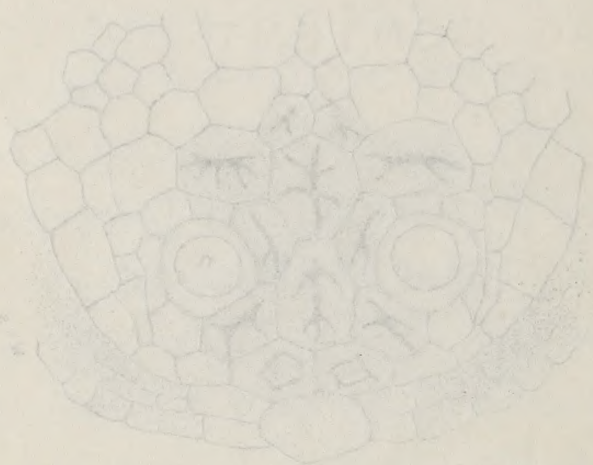
In another section of this paper, the burrowing habit, which is peculiar to the horned lizards, was described, and it was pointed out that the nasal openings of these animals are provided with a mechanism which permits the lizard to breathe easily when the head is below the surface of the ground. This mechanism is quite similar to the one responsible for the distension of the sinus orbitalis. The rather lengthy nasal passage or vestibule is lined with stratified squamous epithelium. Outside of the epithelium the external nares are completely surrounded by a spongy layer which becomes thicker around the posterior margin of the opening. The sinus vestibuli nasi consists of a network of blood spaces which readily throughout the spongy structure. When the sinus vestibuli nasi is distended the spongy tissue swells and closes the nasal opening to such an extent that sand grains and other foreign bodies are prevented from entering the olfactory chamber.

According to Bruner, "When the eye of the lizard is protruded, a sympathetic swelling may sometimes be observed in the region of the sinus vestibuli nasi". In addition to a sympathetic swelling in this region, there is provision for local control of the sinus, and the external nasal openings may be constricted or closed without interfering with the other functions of the head. The local control of the sinus is probably vested in the smooth muscle fibers of the blood vessels.



Rostrum and Nasal Openings of Phrynosoma cornutum

The openings are almost closed by a spongy tissue, which forms a prominent cushion, n, at the posterior margin of each opening. ×4 (after Bruner)



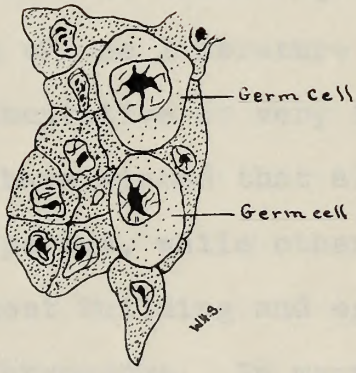
EMBRYOLOGICAL ASPECTS

The Segregation of the Germ-Cells of Phrynosoma cornutum

In a study of a series of Phyrnosoma embryos, M. M. Jarvis found that the peritoneum of the germ-gland anlagen is distinctly thickened throughout the region of the mesonephros, and within these thickenings there are large, rounded cells, composed of clear cytoplasm containing yolk and large clear nuclei with deep-staining chromatin granules. These cells are believed to be typical germ-cells, and their characters are taken as criteria in studying the germ-cells occurring in various parts of the embryow. According to Jarvis, the germ-cells first appear in the entoblast of the vascular area of the blastoderm, and they are located cephalad, caudad, and laterad to the embryo. From this vascular area, most of the germ-cells migrate through the entoblast of the yolk-stalk, intestine, and sclerotome of the mesentery to the germinal anlagen. Some of the cells "lose the way" and segregate to various parts of the embryo, particularly in the sclerotome around the aorta.

Jarvis believes that some of the abnormally placed germ-cells degenerate. In the region of the sclerotome around the aorta, there are cells which represent germ-cells in every respect except the size of the nuclei, which, if present, is about equal to the somatic nuclei. That these cells are transitional forms between the somatic and germ-cells seems to be precluded by the fact that they cannot be found in either the

normal path of migration or the germinal anlagen.



Germ Cells in the Peritoneum of Phrynosoma cornutum

(after Jarvis)

Germ Cells in the Peritoneum of Phrynosoma cornutum

(after Gerry)

SUMMARY

The original plan of this thesis was divided into four major parts, namely: (1) classification; (2) natural history; (3) physiology; (4) morphology. As far as possible, this plan has been followed, but lack of extensive information has prevented the complete discussion of each topic. In the preceding pages the author has attempted to present the known facts about Phrynosoma, and in many instances the information is limited because of the absence of knowledge concerning the particular subject. Much of the literature pertaining to Phrynosoma is either argumentative or very indefinite. For example, several writers have stated that all members of the genus Phrynosoma are viviparous, while other writers have given a description the nest building and egg laying habits of an oviparous species of Phrynosoma. In many similar cases the herpetologists have succumbed to the folly of formulating a generalization for the entire genus, after having made observations on several, and sometimes only on one, species. The author of this monograph has attempted, whenever possible, to indicate certain facts which seem to be applicable to all members of the genus Phrynosoma, and special care has been taken to specify which species were involved in the experiments or observations.

As stated at the end of the section on classification, "...more specific data are necessary before the various species of horned lizards can be assigned to their proper taxonomic

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The original plan of this thesis was divided into four major parts, namely: (1) classification; (2) natural history; (3) physiology; (4) morphology. As far as possible, this plan has been followed, but lack of extensive information has prevented the complete discussion of each topic. In the preceding pages the author has attempted to present the known facts about Phrynosoma, and in many instances the information is limited because of the absence of knowledge concerning the particular subject. Much of the literature pertaining to Phrynosoma is either erroneous or very indefinite. For example, several writers have stated that all members of the genus Phrynosoma are viviparous, while other writers have given a description the nest building and egg laying habits of an oviparous species of Phrynosoma. In many similar cases the herpetologists have succumbed to the folly of formulating a generalization for the entire genus, after having made observations on several, and sometimes only on one, species. The author of this monograph has attempted, whenever possible, to indicate certain facts which seem to be applicable to all members of the genus Phrynosoma, and special care has been taken to specify which species were involved in the experiments or observations.

As stated at the end of the section on classification, "...more specific data are necessary before the various species of horned lizards can be assigned to their proper taxonomic

group". For the most part, the size, character, and arrangement of the spines and scales on the body offer an index to classification, but in final analysis these characters become confusing. A classification based upon osteological characters seems to be the most dependable and logical approach to the taxonomic evaluation of the species of Phrynosoma, but only a few species have been studied in detail.

The natural history of the horned lizards has been sadly neglected. We know that they are a wonderful adaptation to the semi-arid regions, and yet the naturalist, the morphologist, and the physiologist have not become curious enough to probe into the problems concerned with this adaptation. We have been satisfied with the fact that these little creatures are limited in their distribution, that they can endure extreme conditions of heat, that they spurt blood from their eyes, but the question still remains -- WHY?

Our most certain information is concerned with the physiological aspects of the horned lizards. Jordan and Speidal, in their work on blood cell formation, have presented some interesting facts which physiologically place the horned lizards in an intermediate group between the Amphibia and the Reptilia in general. Redfield has made an extensive study of the physiology of the melanophores of horned lizards, and his work indicates the ease with which these animals can be utilized for physiological experiments. Bruner has described a swell mechanism which throws some light upon the moulting, blood spurting, and sub-

terranean habits of the horned lizards. These scientists have given us a clue to many of the problems involved in the life processes of the horned lizards, and future work ought to bring us nearer the solution of these interesting problems.

The fourth division of the original plan has not been written, because there is almost no available information upon the subject. Much research has been done upon the anatomy, embryology, and histology of the European lizard, Lacerta viridis, but, for some reason or another, the American lizard, Phrynosoma, has been neglected. The author hopes that, after the completion of this monograph, he can probe into the structure of the horned lizards, and begin the work which will lead to a more thorough knowledge of these animals of the desert.

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